PRINCIPAL COMPONENTS ANALYSIS OF BIOGEOGRAPHIC PATTERNS AMONG *HELICONIA* INSECT COMMUNITIES

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Abstract.—This study explores biogeographic patterns among insect communities which live in the water-filled floral bracts of *Heliconia* plants. Twenty-five collections from 13 Neotropical locations are studied using a principal components analysis where the collections are ordinated on the basis of the frequency of occurrence of the 23 most common insect morpho species. *Heliconia* species from the French Antilles show a depauperate insect community, apparently due to island isolation. Floral structure is important in determining the insect community: *Heliconia* species with small floral bracts have low species richness and only one *Heliconia* species with a pendant inflorescence has an aquatic or semi-aquatic insect community. Different *Heliconia* species collected from the same location do not necessarily have comparable insect species communities.

Introduction

Biogeographic studies have held an important position in the growth and understanding of evolutionary ecology since the work of Darwin (1859) and Wallace (1876). These studies have attempted to discern patterns of distributions and to identify the factors which determine the distributions of either taxonomically or ecologically related organisms (Price 1975; Pianka 1978). This paper is a biogeographic study based on a principal components analysis (Pielou 1977) of collections of 25 different insect communities living in the water-filled floral bracts of *Heliconia* (Zingiberales: Musaceae) plants collected from 13 different locations in Costa Rica, northern South America and the Antilles made over a period of 8 years. Through this analysis I tried to discern basic biogeographic patterns of *Heliconia* insect communities, to determine if *Heliconia* species in the same location had similar insect communities even if they bloomed during different seasons and to determine if similar insect communities lived in the water-filled bracts of *Heliconia* species with similar bract morphologies.

Plants in the genus *Heliconia* are common members of low- and midelevation Neotropical wet forests. These plants are most frequent in sunlit areas. Detailed studies on the natural history of these plants have been published by Stiles (1975, 1979). Many *Heliconia* species have inflorescences consisting of a series of large erect cup like floral bracts, each bract containing several flowers (Fig. 1). The erect bracts collect and hold both rainwater and water actively pumped into the bracts by the plant (Seifert



Fig. 1. An inflorescence of Heliconia cf. caribaea sp. 2 from Limóncocha, Ecuador.

and Seifert 1976). A diverse group of insects live all or part of their lives in the water-filled *Heliconia* bracts (Seifert 1975; Seifert and Seifert 1976). The insect species composition varies with *Heliconia* species and depends in part on the flowering season of the *Heliconia* species as well as the proportion of the bract which has standing water (Seifert 1980). Some *Heliconia* species have inflorescences which are pendant rather than erect. In most cases, the bracts of pendant species do not hold water or harbor an aquatic insect community. However, one pendant species (*H. rostrata* Ruiz and Pavon) has tightly compressed bracts which retain water and maintain a community of insects similar to that found in some erect bract *Heliconia* species.

Materials and Methods

Twenty-five Heliconia insect communities were collected from different Heliconia species from Costa Rica (2 locations), Venezuela (5 locations), Ecuador (3 locations), Trinidad (1 location), Martinique (1 location) and Guadeloupe (1 location) (Table 1). In 3 cases I collected insect communities from the same *Heliconia* species at the same location in both the early and late portions of the blooming season. At some sites I was able to make collections of more than 1 Heliconia species. In each collection I sampled at least 20 inflorescences, carefully dissected each bract and recorded the number of individuals of each insect species in each inflorescence. After all collections were made, I identified (to genus or family) the 23 insect "morpho species" found most commonly in the collections. For this study, insect morpho species were recorded as ecological equivalents. Thus, for example, there was a category for small hispine beetle (genus Cephaloleia) and I recorded this as present from several collections even though different hispine species existed at different locations. I assumed that the small hispines represented organisms foraging in the same manner even though their Latin binomens differed. Further, in the case of hispine beetles, I recorded adults and larvae separately since in some hispine species only the larvae feed on the inflorescences (Strong 1977a, b; Seifert and Seifert 1979). Next I computed the frequency of occurrence of each insect morpho species in each collection. This figure was simply the number of inflorescences which had at least one specimen of a given insect morpho species divided by the total number of inflorescences in the collection. Following this, a matrix of insect morpho species frequencies (columns) for each Heliconia collection (rows) was constructed (Table 2). These data were analyzed using a principal components analysis which examined the similarity of collections based on their insect morpho species frequencies (R technique of Pielou 1977).

Principal components analysis is an ordination method which is used to examine the pattern of variation among variates where no a priori patterns of causality are suggested. This technique shows relationships among samples which are not apparent from a simple inspection of the data. The original data are projected onto a plot (or series of plots) of few dimensions in such a way that the arrangement of points suffers the least possible distortion. Each principal component is a linear combination of the original vari-

| Collection label | Heliconia species resemblance and describer | Collection location | Approximate co-ordinants | Season collected |
|---------------------|--|----------------------------|-----------------------------|---------------------|
| 1 | <i>aurea</i> Rodríguez | Rancho Grande Venezuela | 10°21'N 65°41'W | wet season |
| 2 | cf. <i>humilis</i> sp. 1 Jacq. | La Escalera Venezuela | 05°45′N 61°25′W | wet season |
| 3 | cf. <i>humilis</i> sp. 2 Jacq. | El Dorado Venezuela | 06°41′N 61°35′W | wet season |
| 4 | cf. <i>caribaea</i> sp. 2 Lamarck | Limóncocha Ecuador | 0°34′S 76°38′W | dry season |
| 5 | cf. <i>humilis</i> sp. 3 Jacq. | Primavera Ecuador | 0°32′S 76°45′W | dry season |
| 6 | <i>episcopalis</i> Velloso | Primavera Ecuador | 0°32′S 76°45′W | dry season |
| 7 | <i>bihai</i> Linn. | Les Nuages Martinique | 14°42′N 61°06′W | wet season |
| 8 | cf. <i>caribaea</i> sp. 1 Lamarck | Panaquire Venezuela | 10°21'N 66°15'W | wet season |
| 9 | <i>bihai</i> Linn. | Bains Juanes Guadeloupe | 16°03'N 61°40'W | wet season |
| 10 | <i>caribaea</i> Lamarck | Les Nuages Martinique | 14°42′N 61°06′W | wet season |
| 11 | <i>caribaea</i> Lamarck | Bains Juanes Guadeloupe | 16°03′N 61°40′W | wet season |
| 12 | cf. <i>caribaea</i> sp. 1 Lamarck | La Trilla Venezuela | 10°22'N 65°42'W | wet season |
| 13 | <i>rostrata</i> Ruiz and Pavon | Limóncocha Ecuador | 0°34′S 76°38′W | dry season |
| 14 | <i>latispatha</i> Bentham | Tinalandia Ecuador | 0°14′S 79°07′W | dry season |
| 15 | cf. <i>caribaea</i> sp. 1 Lamarck | Guatopo Venezuela | 09°45′N 66°28′W | wet season |
| 16 | rodriguensis Aristeguieta | Guatopo Venezuela | 09°45′N 66°28′W | wet season |

Table 1. Collection label, *Heliconia* species resemblance, collection location and season of collection for 25 *Heliconia* collections used in the principle components analysis.

| Collection label | Heliconia species resemblance and describer | Collection location | Approximate co-ordinants | Season collected |
|------------------|--|-----------------------------|-----------------------------|-----------------------|
| 17 | <i>bihai</i> Linn. | Rancho Grande Venezuela | 10°21'N 65°41'W | dry season (early) |
| 18 | <i>bihai</i> Linn. | Rancho Grande Venezuela | 10°21′N 65°41′W | wet season (late) |
| 19 | <i>imbricata</i> (Kuntze) Baker | Rincón de Osa Costa Rica | 08°42′N 83°30′W | wet season (early) |
| 20 | <i>imbricata</i> (Kuntze) Baker | Rincón de Osa Costa Rica | 08°42′N 83°30′W | wet season (late) |
| 21 | <i>wagneriana</i> Petersen | Rincón de Osa Costa Rica | 08°42′N 83°30′W | dry season (early) |
| 22 | <i>wagneri<mark>a</mark>na</i> Petersen | Rincón de Osa Costa Rica | 08°42'N 83°30'W | dry season (late) |
| 23 | <i>latispatha</i> Bentham | Sirena Costa Rica | 08°40' N 83°40' W | dry season |
| 24 | <i>wagneriana</i> Petersen | Sirena Costa Rica | 08°40' N 83°40' W | dry season |
| 25 | cf. <i>caribaea</i> sp. 1 Lamarck | Simla Trinidad | 10°45′N 61°22′W | wet season |

| Tabl | le 1 | l. I | Cont | inu | ed. |
|------|------|------|------|-----|-----|
| | | | | | |

NOTE: The taxonomic status and nomenclature of many members of the genus *Heliconia* are uncertain. Identifications follow, when possible, Aristeguieta (1961) and Daniels and Stiles (1979). *Heliconia* species designated as *H*. cf. *caribaea* and *H*. cf. *humilis* represent morphological forms, some of which may be undescribed, which appear similar to members of the *H*. *caribaea* and *H*. *humilis* species complexes. However, only the forms from Martinique and Guadeloupe represent true populations of the species originally described as *H*. *caribaea* Lamarck.

ates where the first principal component accounts for the maximum possible variance and each subsequent component accounts for a decreasing amount of the residual variance. In this study each of the 25 *Heliconia* collections is characterized by the frequency of occurrence of the 23 morpho species. The *Heliconia* collections represent the variates to be ordinated; the insect morpho species frequencies are the attributes on which the ordination is based. Principal components analysis has been used frequently in taxonomic studies (Sneath and Sokal 1973) as well as in ecological studies (Pielou 1977). Often the characters used are standardized when the variates are measured in different units. However, in ecological work when the variates are measured in the same units (here, frequencies of insect morpho species) standardization is not appropriate (Pielou 1977). Further, some workers, partic-

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|---|---|---|
| T | T | - |

| Heliconia | | | | | Insect n | norpho sp | ecies fre | quencies | | | | |
|---------------------|------|------|------|------|----------|-----------|-----------|----------|------|------|------|------|
| collection label | а | b | с | đ | e | f | g | h | i | j | k | 1 |
| 1 | 0.91 | 0.14 | 0.84 | 0.02 | 0.28 | 0.97 | 0.14 | 0.00 | 0.22 | 0.09 | 0.03 | 0.02 |
| 2 | 0.85 | 0.40 | 0.35 | 0.00 | 0.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 |
| 3 | 1.00 | 0.55 | 0.10 | 0.65 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.05 |
| 4 | 0.79 | 0.88 | 0.09 | 0.02 | 0.21 | 0.40 | 0.26 | 0.54 | 0.37 | 0.26 | 0.09 | 0.00 |
| 5 | 0.77 | 0.60 | 0.00 | 0.13 | 0.57 | 0.10 | 0.43 | 0.27 | 0.00 | 0.13 | 0.00 | 0.00 |
| 6 | 0.00 | 0.61 | 0.00 | 0.00 | 0.79 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 0.00 | 0.00 | 0.00 | 0.18 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 |
| 8 | 1.00 | 0.17 | 0.27 | 0.67 | 0.57 | 0.73 | 0.30 | 0.00 | 0.20 | 0.03 | 0.00 | 0.00 |
| 9 | 0.00 | 0.00 | 0.48 | 0.31 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 | 0.10 | 0.00 |
| 10 | 0.52 | 0.00 | 0.00 | 0.77 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 11 | 0.00 | 0.00 | 0.58 | 0.93 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 |
| 12 | 1.00 | 0.83 | 0.64 | 0.93 | 0.80 | 0.23 | 0.00 | 0.03 | 0.00 | 0.17 | 0.00 | 0.00 |
| 13 | 0.00 | 0.79 | 0.00 | 0.10 | 0.69 | 0.00 | 0.07 | 0.21 | 0.07 | 0.45 | 0.00 | 0.03 |
| 14 | 0.68 | 0.77 | 0.10 | 0.00 | 0.39 | 0.00 | 0.32 | 0.00 | 0.32 | 0.06 | 0.16 | 0.00 |
| 15 | 1.00 | 0.85 | 0.50 | 0.80 | 0.25 | 0.30 | 0.05 | 0.00 | 0.00 | 0.10 | 0.00 | 0.00 |
| 16 | 0.82 | 0.71 | 0.52 | 0.94 | 0.09 | 0.15 | 0.03 | 0.12 | 0.35 | 0.12 | 0.03 | 0.03 |
| 17 | 0.59 | 0.66 | 0.94 | 0.28 | 0.03 | 0.88 | 0.41 | 0.12 | 0.19 | 0.59 | 0.28 | 0.00 |
| 18 | 0.12 | 0.70 | 0.79 | 0.18 | 0.00 | 1.00 | 0.24 | 0.09 | 0.42 | 0.39 | 0.09 | 0.03 |
| 19 | 0.83 | 0.80 | 0.30 | 0.93 | 0.47 | 0.70 | 0.50 | 0.03 | 0.03 | 0.23 | 0.20 | 0.73 |
| 20 | 0.40 | 0.80 | 0.37 | 0.87 | 0.33 | 0.83 | 0.17 | 0.43 | 0.00 | 0.27 | 0.13 | 0.53 |
| 21 | 0.10 | 0.97 | 0.43 | 0.03 | 0.00 | 0.07 | 0.37 | 0.00 | 0.00 | 0.13 | 0.03 | 0.03 |
| 22 | 0.83 | 0.67 | 0.77 | 0.37 | 0.97 | 0.00 | 0.07 | 0.67 | 0.00 | 0.60 | 0.07 | 0.27 |
| 23 | 0.60 | 0.07 | 0.13 | 0.00 | 0.27 | 0.00 | 0.73 | 0.00 | 0.00 | 0.13 | 0.00 | 0.00 |
| 24 | 0.95 | 0.90 | 0.90 | 0.05 | 0.90 | 0.10 | 0.16 | 0.32 | 0.00 | 0.26 | 0.00 | 0.00 |
| 25 | 0.85 | 0.20 | 0.10 | 0.05 | 0.20 | 0.10 | 0.00 | 0.00 | 0.35 | 0.10 | 0.05 | 0.00 |

Table 2. Frequency of occurrence of the 23 most common insect "morpho species" (listed by letters) found in 25 *Heliconia* inflorescences collections.

NOTE: The *Heliconia* collection labels are the same as those listed in Table 1. Insects represented by letters are: a = Quichuana (Syrphidae), b = Gillisius (Hydrophilidae), c = copestylum (Syrphidae), d = Merosargus (Stratiomyidae), e = Beebeomyia (Richardiidae), f = Cephaloleia larva (Chrysomelidae), g = Cephaloleia adult (Chrysomelidae), h = small Gillisius (Hydrophilidae), i = large hispine (Chrysomelidae), j = Odontolinus (Staphylinidae),

ularly in taxonomic studies, remove highly correlated characters. Once again this procedure is less commonly used in ecological work where high correlations of insect frequencies may indicate a particular and regular pattern of community structure. I have constructed a correlation matrix based on insect morpho species frequencies (Table 3). However, insect morpho species whose frequencies are highly correlated were not removed from the data set used to produce this principal components analysis. My procedure (no standardization, no removal of correlated characters) follows Pielou (1977) who can be referred to for a more detailed treatment of principal components analysis in ecological studies. Thus, the data set which I use in this principal components analysis is the *Heliconia* collection by insect morpho species frequencies listed in Table 2.

| Table 2. Co | ntinued. |
|-------------|----------|
|-------------|----------|

| <i>Heliconia</i> collection | | | | | Insect n | norpho sp | ecies fre | quencies | | | |
|-----------------------------|------|------|------|------|----------|-----------|-----------|----------|------|------|------|
| label | m | n | 0 | р | q | r | s | t | u | v | w |
| 1 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 | 1.00 | 0.57 | 0.00 |
| 2 | 0.05 | 0.00 | 0.00 | 0.00 | 0.15 | 0.00 | 0.00 | 0.55 | 0.00 | 0.00 | 0.00 |
| 3 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 0.20 | 0.00 | 0.40 |
| 4 | 0.02 | 0.00 | 0.16 | 0.00 | 0.19 | 0.02 | 0.09 | 0.59 | 0.00 | 0.00 | 0.00 |
| 5 | 0.03 | 0.00 | 0.00 | 0.00 | 0.07 | 0.00 | 0.03 | 0.90 | 0.00 | 0.00 | 0.00 |
| 6 | 0.03 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.68 | 0.00 | 0.00 |
| 8 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 0.97 | 0.20 | 0.00 | 0.17 |
| 9 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.19 | 0.00 | 0.00 |
| 10 | 0.00 | 0.03 | 0.03 | 0.00 | 0.00 | 0.03 | 0.00 | 0.03 | 0.87 | 0.00 | 0.00 |
| 11 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | . 0.00 | 1.00 | 0.00 | 0.00 |
| 12 | 0.00 | 0.30 | 0.33 | 0.03 | 0.00 | 0.00 | 0.00 | 0.97 | 0.00 | 0.00 | 0.00 |
| 13 | 0.00 | 0.03 | 0.21 | 0.00 | 0.00 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 14 | 0.03 | 0.00 | 0.39 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 15 | 0.00 | 0.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.60 | 0.00 | 0.00 | 0.00 |
| 16 | 0.00 | 0.09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.91 | 0.00 | 0.00 | 0.00 |
| 17 | 0.00 | 0.00 | 0.09 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 18 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 19 | 0.00 | 0.00 | 0.17 | 0.07 | 0.00 | 0.00 | 0.17 | 0.77 | 0.00 | 0.00 | 0.00 |
| 20 | 0.00 | 0.00 | 0.17 | 0.03 | 0.00 | 0.03 | 0.10 | 0.73 | 0.00 | 0.00 | 0.00 |
| 21 | 0.00 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 |
| 22 | 0.20 | 0.07 | 0.43 | 0.00 | 0.00 | 0.03 | 0.03 | 0.83 | 0.00 | 0.00 | 0.00 |
| 23 | 0.07 | 0.20 | 0.47 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 24 | 0.00 | 0.21 | 0.05 | 0.00 | 0.05 | 0.00 | 0.21 | 0.73 | 0.79 | 0.00 | 0.00 |
| 25 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.75 | 0.00 | 0.00 | 0.15 |

k = Carcinophora (Carcinophoridae), 1 = cockroach (Blattidae), m = Noctuidae, n = Pyralidae, o = small Staphylinidae, p = tiny Staphylinidae, q = Scarabidae, r = Curculionidae, s = Carabidae, t = Wyeomyia (Culicidae), u = Culex (Culicidae), v = Trichoprosopon (Culicidae), w = Toxorhynchites (Culicidae).

Results

The first 3 components accounted for a total of 68.13% of the variation of *Heliconia* insect communities. The component weights for each of the first 3 components are listed in Table 4. Component 1 weights most heavily, in decreasing order of weight, on *Quichuana* (Diptera: Syrphidae), *Gillisius* (Coleoptera: Hydrophilidae) and *Wyeomyia* (Diptera: Culicidae). These are the most frequently encountered and abundant insect species in many *Heliconia* inflorescences. The frequencies of *Quichuana* and *Wyeomyia* are positively correlated in *Heliconia* collections (Table 3). Component 2 weighs most heavily on *Culex* (Diptera: Culicidae), *Merosargus* (Diptera: Stratiomyidae) (a negative weight) and *Copestylum* (Diptera: Syrphidae) (a negative weight). This component weighs most heavily on a second group

| Insect morpho | | | | | I | nsect mor | pho specie | es | | | | |
|------------------|--------|--------|--------|--------|--------|-----------|------------|--------|--------|--------|--------|--------|
| species | a | b | с | d | e | f | g | h | i | j | k | 1 |
| а | 1.000 | | | | | | | | | | | |
| b | 0.306 | 1.000 | | | | | | | | | | |
| с | 0.176 | 0.262 | 1.000 | | | | | | | | | |
| đ | 0.197 | 0.077 | 0.139 | 1.000 | | | | | | | | |
| e | 0.313 | 0.287 | 0.043 | -0.071 | 1.000 | | | | | | | |
| f | 0.170 | 0.201 | 0.467 | 0.159 | -0.104 | 1.000 | | | | | | |
| g | 0.115 | 0.214 | -0.023 | -0.228 | 0.013 | 0.309 | 1.000 | | | | | |
| h | 0.142 | 0.466 | 0.172 | -0.066 | 0.438 | 0.085 | 0.052 | 1.000 | | | | |
| i | 0.154 | 0.153 | 0.103 | -0.202 | -0.247 | 0.420 | 0.098 | 0.046 | 1.000 | | | |
| j | -0.015 | 0.518 | 0.485 | -0.076 | 0.281 | 0.347 | 0.239 | 0.652 | 0.155 | 1.000 | | |
| k | -0.014 | 0.286 | 0.276 | -0.010 | -0.207 | 0.496 | 0.360 | 0.157 | 0.313 | 0.493 | 1.000 | |
| 1 | 0.080 | 0.301 | 0.042 | 0.418 | 0.189 | 0.361 | 0.238 | 0.308 | -0.186 | 0.284 | 0.460 | 1.000 |
| m | 0.264 | -0.084 | -0.077 | -0.261 | 0.302 | -0.327 | -0.062 | 0.368 | 0.039 | 0.236 | -0.041 | 0.055 |
| n | 0.188 | 0.292 | 0.257 | 0.064 | 0.388 | -0.258 | 0.105 | -0.010 | -0.313 | 0.036 | -0.376 | -0.166 |
| 0 | 0.160 | 0.259 | 0.004 | -0.064 | 0.441 | -0.108 | 0.397 | 0.368 | -0.035 | 0.418 | 0.204 | 0.243 |
| р | 0.167 | 0.309 | 0.036 | 0.516 | 0.217 | 0.350 | 0.216 | 0.038 | -0.199 | 0.106 | 0.378 | 0.843 |
| q | 0.246 | 0.205 | -0.139 | -0.351 | 0.016 | -0.083 | 0.033 | 0.377 | 0.132 | -0.042 | 0.002 | -0.150 |
| r | -0.294 | 0.148 | -0.059 | 0.081 | 0.129 | -0.001 | -0.120 | 0.491 | -0.086 | 0.578 | 0.139 | 0.157 |
| s | 0.070 | 0.289 | 0.036 | -0.039 | 0.496 | 0.147 | 0.210 | 0.331 | -0.180 | 0.082 | 0.090 | 0.462 |
| t | 0.788 | 0.278 | 0.221 | 0.305 | 0.440 | 0.282 | -0.069 | 0.325 | 0.099 | 0.007 | -0.136 | 0.281 |
| u | -0.115 | -0.497 | 0.180 | 0.092 | -0.182 | -0.035 | -0.303 | -0.193 | -0.185 | -0.325 | -0.314 | -0.205 |
| v | 0.179 | -0.215 | 0.315 | -0.196 | -0.033 | 0.411 | -0.033 | 0.125 | 0.170 | -0.104 | -0.055 | -0.060 |
| w | 0.336 | -0.108 | -0.244 | 0.143 | -0.073 | -0.068 | -0.168 | -0.201 | 0.041 | -0.225 | -0.198 | -0.077 |

Table 3. Matrix of pairwise correlations among the frequencies of occurrence of 23 insect morpho species from 25 different *Heliconia* collections.

of commonly encountered species all of which are mosquito and fly species. Component 3 weighs most heavily on insects associated with the first two components: *Copestylum* (a negative weight), *Gillisius* (a negative weight) and *Wyeomyia*.

The results of the principal components analysis are presented graphically in Figures 2, 3 and 4. Figure 2 shows a plot of component 1 versus component 2. The collections from the French Antilles (10, 7, 9, 11) are grouped in the lower left region of the graph. These collections have low insect species richness. In particular, hydrophilid, hispine and staphylinid beetles which are common members of many Heliconia insect communities, are not found in the island collections. Further, in 3 of the collections (7, 9, 11) only 1 genus of mosquito (Culex) was recorded, while up to 4 genera are sometimes found in mainland collections. On the right edge of the graph are collections (24, 12, 15, 8, 3) from various locations which, with the exception of H. wagneriana Petersen (24), have morphologies similar to H. cf. caribaea Lamarck (Fig. 1). This graph also shows close association of insect community structure among collections of the same Heliconia species from the same locations. Thus, both the early (17) and late (18) collections of H. bihai L. from Rancho Grande (Venezuela), the early (19) and late (20) collections of *H. imbricata* (Kuntze) Baker and Rincón de Osa (Costa Rica)

VOLUME LXXXIX, NUMBER 2

| Insect | | | | | I | nsect mor | pho speci | es | | | | |
|-------------------|--------|--------|--------|--------|--------|-----------|-----------|--------|--------|-------|-------|--|
| morpho species | m | n | 0 | р | q | r | s | t | u | v | w | |
| а | | | | | | | | | | | | |
| b | | | | | | | | | | | | |
| с | | | | | | | | | | | | |
| d | | | | | | | | | | | | |
| e | | | | | | | | | | | | |
| f | | | | | | | | | | | | |
| g | | | | | | | | | | | | |
| h | | | | | | | | | | | | |
| i | | | | | | | | | | | | |
| j | | | | | | | | | | | | |
| k | | | | | | | | | | | | |
| 1 | | | | | | | | | | | | |
| m | 1.000 | | | | | | | | | | | |
| n | -0.035 | 1.000 | | | | | | | | | | |
| 0 | 0.385 | 0.375 | 1.000 | | | | | | | | | |
| р | -0.180 | 0.104 | 0.249 | 1.000 | | | | | | | | |
| q | 0.043 | -0.123 | -0.077 | -0.133 | 1.000 | | | | | | | |
| r | 0.046 | -0.187 | 0.264 | -0.029 | -0.006 | 1.000 | | | | | | |
| s | -0.121 | 0.166 | -0.040 | 0.410 | 0.194 | -0.092 | 1.000 | | | | | |
| t | 0.205 | 0.118 | -0.013 | 0.324 | 0.197 | -0.224 | 0.222 | 1.000 | | | | |
| u | -0.274 | -0.077 | -0.326 | -0.197 | -0.118 | 0.014 | -0.005 | -0.068 | 1.000 | | | |
| v | -0.107 | -0.126 | -0.117 | -0.071 | -0.079 | -0.114 | -0.125 | -0.289 | 0.474 | 1.000 | | |
| w | 0.229 | -0.203 | -0.227 | -0.114 | -0.127 | -0.184 | -0.117 | -0.187 | -0.037 | 0.067 | 1.000 | |

| rable 5. Commuteu. | Table | 3. | Continued. |
|--------------------|-------|----|------------|
|--------------------|-------|----|------------|

and the early (21) and late (22) collections of *H. wagneriana* from Rincón de Osa are located close to one another.

Considering Figure 3 next, which plots component 1 versus component 3, much of the same clustering as in Figure 2 is shown. *Heliconia* species which were collected twice from the same location cluster together, *Heliconia* species with morphologies similar to *H*. cf. *caribaea* cluster together and the Antillean collections border the left side of the graph. Here, however, the Antillean collections (10, 7, 11, 9) enclosed the collection of *H. episcopalis* Velloso from Primavera, Ecuador (6). *H. episcopalis* is a species with small floral bracts and contains few insects. Thus, the generation of low insect diversity *Heliconia* plants occurs both because of the isolation of some *Heliconia* species on islands and because of the small inflorescence size of *H. episcopalis*.

The final graph, Figure 4, which compares component 2 versus component 3, again shows groupings of the species from the Antilles, clustering of collections of the same *Heliconia* species collected at different times and clustering of *Heliconia* species with similar floral morphologies. Figure 4, however, also shows that *H. rostrata* from Limóncocha, Ecuador (13) lies on the right side of the graph rather distant from most other collections. *H. rostrata* represents the only *Heliconia* species studies which had pendant

| nsect morpho – | | Compone | nt number | |
|----------------|-------|---------|-----------|--------|
| species | 1 | 2 | 3 | 4 |
| а | 0.667 | -0.034 | 0.125 | -0.049 |
| b | 0.546 | 0.097 | -0.188 | 0.074 |
| с | 0.360 | -0.128 | -0.191 | 0.006 |
| d | 0.374 | -0.245 | 0.031 | 0.011 |
| e | 0.340 | 0.083 | 0.056 | 0.204 |
| f | 0.270 | -0.055 | -0.167 | -0.150 |
| g | 0.162 | 0.053 | -0.065 | 0.002 |
| h | 0.126 | 0.042 | -0.029 | 0.035 |
| i | 0.103 | 0.014 | -0.034 | -0.050 |
| j | 0.169 | 0.028 | -0.114 | 0.037 |
| k | 0.052 | -0.000 | -0.044 | -0.013 |
| 1 | 0.080 | -0.001 | -0.030 | -0.013 |
| m | 0.027 | 0.011 | 0.016 | 0.006 |
| n | 0.052 | 0.005 | -0.006 | 0.035 |
| 0 | 0.100 | 0.047 | -0.017 | 0.056 |
| р | 0.007 | -0.001 | -0.002 | -0.001 |
| q | 0.023 | 0.010 | 0.007 | -0.003 |
| r | 0.008 | -0.000 | -0.006 | 0.007 |
| s | 0.037 | 0.007 | -0.003 | 0.020 |
| t | 0.527 | -0.039 | 0.142 | -0.079 |
| u | 0.117 | -0.290 | 0.039 | 0.113 |
| v | 0.020 | -0.024 | 0.007 | -0.018 |
| W | 0.035 | -0.010 | 0.029 | -0.015 |

Table 4. Component weights on 23 insect morpho species from 25 Heliconia collections.

NOTE: Insects listed by letters follow the same sequence as that listed in Table 2.

inflorescences but still contained an aquatic insect community. While this community includes many of the common insects, it is unusual in that neither syrphid fly genera nor hispine beetle larvae were represented in the collection.

Discussion

The principal components weigh heavily on some of the most common fly, mosquito and beetle species. This implies that much of the variation in these insect communities from the 25 *Heliconia* collections is dependent on differences in *Quichuana*, *Gillisius*, *Wyeomyia*, *Culex*, *Merosargus* and *Copestylum* frequencies. The resulting placement of the 25 *Heliconia* collections on the principal components analysis graphs (Figs. 2, 3, 4) can be interpreted in relationship to knowledge about *Heliconia* collection localities, bract morphologies and flowering phenologies. The principal components analysis shows most clearly the similarity of the depauperate fauna of *Heliconia* inflorescences from the Antilles. Low species richness among

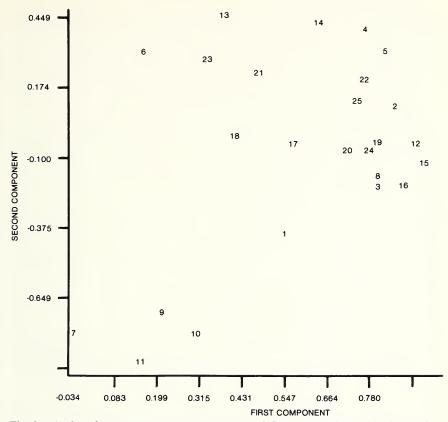


Fig. 2. A plot of component 1 versus component 2 for 25 collections of *Heliconia* insect communities. The numbers are the same as those listed in Table 1.

island biota is a commonly observed phenomenon (MacArthur and Wilson 1967; Carlquist 1974). In the case of *Heliconia* insect communities, this reduction of species richness is largely the result of a lack of beetle species and the presence of only 1, instead of several, mosquito species. I suspect that the lack of these insects is simply the result of an inability of some insects to locate, invade and colonize the islands. In Guadeloupe I was able to maintain Ecuadorian hispine species in petri dishes by feeding them bracts of both *H. bihai* Linn. and *H. caribaea* from local *Heliconia* populations. Thus, it seems clear that these beetles could form a breeding population on Guadeloupe. That they have not done so is probably attributable to their low rates of movement. Other research (Beaman 1980) has shown that *Heliconia* feeding hispines move only short distances among *Heliconia* clumps and do not exhibit long range dispersal.

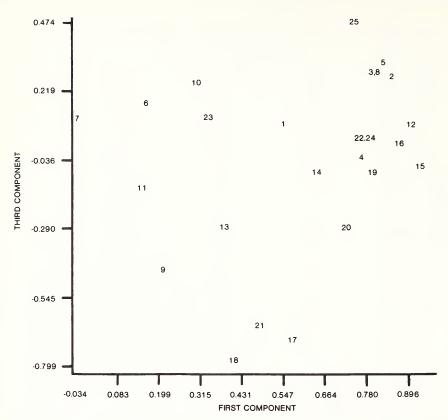


Fig. 3. A plot of component 1 versus component 3 for 25 collections of *Heliconia* insect communities. The numbers are the same as those listed in Table 1.

Further, from this biogeographic work we can interpret that floral morphologies are important in generating particular *Heliconia* insect community structure. Small *Heliconia* species, such as *H. episcopalis*, not only have low species richness but also are devoid of some of the most frequent *Heliconia* inquilines, syrphid fly larvae. Clearly, the kind of floral morphology of pendant *Heliconia* species is also important in determining the *Heliconia* insect community. While most pendant species do not contain an aquatic insect community (Seifert and Seifert 1979; personal observation), *H. rostrata*, because of its compressed bracts, does contain water and harbors some of the insect species associated with other *Heliconia* species. Finally, *Heliconia* with similar morphologies, such as *H. cf. caribaea* species, may contain largely similar *Heliconia* insect communities.

The results of the principal components analysis also point out that *Heliconia* inflorescences of the same species at the same location have similar *Heliconia* insect communities even if they are collected during different portions of the blooming season. The insect community structure, based on

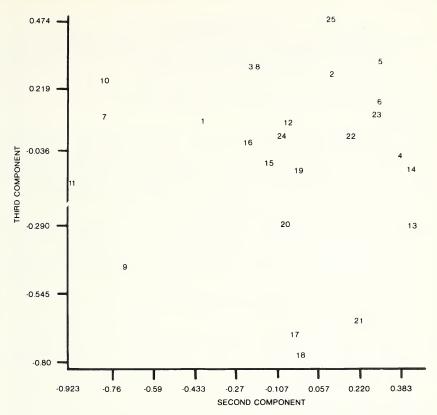


Fig. 4. A plot of component 2 versus component 3 for 25 collections of *Heliconia* insect communities. The numbers are the same as those listed in Table 1.

the presence of at least one individual of each insect species, remains approximately the same throughout much of the blooming season of a *Heliconia* species.

This principal components analysis did not show clustering of different *Heliconia* species from the same location. Thus, *H. aurea* Rodriguez from Rancho Grande (1) did not cluster close to *H. bihai* from Rancho Grande (17, 18), and *H. imbricata* from Rincón de Osa (19, 20) did not cluster with *H. wagneriana* from the same location (21, 22). Only in the cases of the collections from the Antilles, where isolation is important in determining insect species richness, did different *Heliconia* species from the same location show affinities.

In conclusion, this study has shown how principal components analysis can be used to examine the similarity of insect communities living in association with different species of closely related plants from different locations. The results of the analysis indicate the importance of plant isolation and floral morphology in determining insect community structure.

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